SECONDARY PRODUCTION OF HIGHLY UNSATURATED FATTY ACIDS BY ZOOBENTHOS ACROSS RIVERS CONTRASTING IN TEMPERATURE

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ABSTRACT

Highly unsaturated fatty acids (HUFA), namely eicosapentaenoic acid (20:5n-3, EPA) and docosahexaenoic acid (22:6n-3, DHA), which are essential for many animals, including humans are mainly produced in aquatic trophic webs. In fast-flowing rivers macrozoobenthos is the main source of HUFA for fish and may be particularly vulnerable to thermal alterations associated with climate change. We studied benthic communities in a unique natural ecosystem: the Yenisei River downstream of the dam of Krasnoyarsk Hydroelectric Power Station with very low temperature in summer because of discharge of cold water from deep in the reservoir, and its tributaries with high summer temperature. This 'natural experiment' allowed to get rid of confounding factors, such as differences in light, seasonality, geology (biogeochemistry) and biogeography (regional species pools). As found, in spite of an increase of biodiversity and rates of daily production in warm rivers compared to cold sites, DHA and partly EPA production of zoobenthos decreased with increase of temperature because of changes in species composition. Thus, in a climate warming context we can predict a decrease of production of these HUFA by river zoobenthos and thereby a diminishing of their supply for fish and next to humans.

INTRODUCTION

Impacts of global climate warming on the aquatic ecosystems are profound, and thereby complex approaches to predicting their consequences are needed (Woodward et al., 2010). Although many studies of the climate impacts are focused on structural attributes, such as species richness and biodiversity (Woodward et al., 2010), functional responses of ecosystems as sources or sinks in global carbon cycles evidently are of great importance for the complex predicting of consequences of global warming (Perkins et al., 2012).

Besides fluxes of total carbon, production and transfer of particular compounds can be of great importance for ecosystems' functioning. For instance, essential nutrients, highly unsaturated fatty acids (HUFA), which are one of the factors controlling growth and development of many animals, including humans, are produced primarily in aquatic ecosystems by certain microalgae and then are transferred to terrestrial ecosystems through diverse food chains (Gladyshev et al., 2009). Nowadays, the main source of essential HUFA in human's diet is fish. Wild fish catch and aquaculture production have reached their upper limits, but still cannot cover HUFA requirements of humankind (Gladyshev et al., 2013). HUFA content in different fish species range around two orders of magnitude and strongly depend on HUFA sources in their diet (Sargent et al., 1999; Gladyshev et al., 2013). Hence, high HUFA values in biomass of planktonic and benthic invertebrates, as main food sources for fish, are required to maintain proper HUFA content in wild fish catch.

The peculiar 'biosphere service' of aquatic ecosystems as the source of HUFA may be threatened by the climate warming. Indeed, in pelagic ecosystems a decrease of HUFA contents in the main conduit between microalgae and fish, zooplankton, under increased water temperature was found recently (Maazouzi et al., 2008; Gladyshev et al., 2011). In rivers or rivers' stretches with a high current velocity, zoobenthos is the main food source for fish. Nevertheless, there are practically no data on a possible effect of climate warming on HUFA production by river zoobenthos. Note that among aquatic ecosystems, river communities are expected to be particularly vulnerable to thermal alterations associated with climate change (Isaak & Rieman, 2013).

There are several ways of studying the possible effects of the global warming on aquatic ecosystems: i) mesocosm experiments (e.g., Strecker et al., 2004; Hines et al., 2013), ii) long-term series of observations (e.g., Hampton et al., 2008; Floury et al., 2013) and iii) inferential surveys that span large temperature gradients across differences in latitude and altitude (e.g., Jacobsen et al., 1997; Kattner & Hagen, 2009). However, all the above important methods have certain evident shortcomings, namely decreased resemblance of mesocosms to natural

communities, insufficient availability of long-term series, and confounded effects of differences in light, biogeochemistry and biogeography in latitude/altitude surveys (Woodward et al., 2010). Recently some of these difficulties were overcome using a unique natural ecosystem: Icelandic geothermal streams that lie 2 m - 2 km apart and have comparable physico-chemical properties and an identical regional species pool, but strongly vary in temperature (Friberg et al., 2009). This system represents a 'natural experiment' which allowed getting a set of new data on possible effect of global warming on structure and functions of stream ecosystems (Woodward et al., 2010; Perkins et al., 2012).

An opportunity to carry out similar 'natural experiment' also exists in middle reach of the Yenisei River (Siberia, Russia). In summer, water temperature in the main channel of the river about 100 km downstream of the dam of Krasnoyarsk Hydroelectric Power Station is ca.6-12 ^{o}C because of the cold water discharge from deep of the reservoir (Dubovskaya et al., 2004). In contrast, tributaries of the river have usual summer temperatures, ca. 15-22 ^{o}C. Thus, we used this unique ecosystem to study an effect of temperature on production of HUFA by river zoobenthos as the main conduit between primary producers and fish, and thereby to estimate a possible impact of climate warming on the 'biosphere service' of river ecosystems as providers of these essential nutrients.

An increase of water temperature is known to potentially decrease HUFA content in aquatic organisms via several mechanisms (Schlechtriem et al., 2006; Maazouzi et al., 2008; Gladyshev et al., 2011), although it evidently accelerates aquatic production. Thus, the increase of production of biomass may overcome a decrease of HUFA contents in this biomass, and thereby HUFA production in a certain ecosystem may stay at the same level, or even increase under climate warming. Thus, the general aim of our work was to clarify this uncertainty. We focused on two most physiologically important and quantitatively prominent HUFA, eicosapentaenoic acid (20:5n-3, EPA) and docosahexaenoic acid (22:6n-3, DHA) and tested following hypotheses: 1) in a cold river the same taxa have higher levels of EPA and DHA in their biomass than those in a warm river; 2) in a cold river taxa with higher EPA and DHA contents are more abundant; 3) production of EPA and DHA by zoobenthos in a cold river is higher in spite of lower water temperature.

STUDY AREA

The study was carried out in the Yenisei River and two tributaries (Fig. 1). The Yenisei is the longest river (4803 km) and has the greatest water discharge (636 km^3 yr^{-1}) and discharge of organic carbon among all the rivers flowing into the Arctic Ocean (Amon et al., 2012). Detailed

ecological characteristics of the river are given elsewhere (Gladyshev et al., 1993). In middle reach the river is regulated by the dam of Krasnoyarsk Hydroelectric Power Station which passes waters from 20-40 m depth of hypolimnion of the reservoir. The upstream reservoir is deep (ca. 110 m) and thermally stratified and had low phytoplankton biomass and organic carbon in hypolimnetic waters near the dam (Ageev et al., 2008). This results in relatively low phytoplankton biomass, on average 1-2 mg L^{-1} (Ponomareva, 2015) and low particulate organic carbon ranged from 0.13 to 0.25 mg L^{-1} (Sushchik, unpublished data), in downstream river section of about 50 km.

The Mana River, a right tributary of the Yenisei River, and the Kacha River, a left tributary, (Fig. 1), have length 533 and 103 km and average annual discharge of 93 and 4.3 m^3 s^{-1}, correspondingly (Zapekina-Dulkeit & Dulkeit, 1961; Panov & Spitsyna, 2010).

We sampled four sites which located 15-30 km downstream of the dam: the left and right banks of the Yenisei, the Mana and the Kacha (Fig. 1). All sampling sites are upstream of the municipal area of Krasnoyarsk city (Fig. 1), and have similar hydrological characteristics: current velocity 1-2 m s^{-1} and stony beds.

Main primary producers in the rivers are epilithic microalgae and cyanobacteria. Diatom and green taxa mainly comprise ephilithic biofilms in all three rivers, while cyanobacteria sporadically occur in the Yenisei and Kacha (Table 1). There are many common species in all three studied rivers (Table 1).

MATERIAL AND METHODS

The sites were sampled monthly from May to September 2012 and 2013, about 5-10 m from the shore (ca. 0.5-0.7 m of depth). To compare the two shallow rivers, Mana and Kacha, with the large Yenisei River, in the latter we sampled only littoral sites. Water samples for nutrient's analysis were collected with a bucket from the middle of water column. Zoobenthos samples were collected using a Surber sampler (quadrate 40×35 cm, mesh size 0.25 mm). In 2012, one sample was taken from each site per sampling date, and in 2013, three replicates were collected. The samples were transported fresh to the laboratory within 1-2 hours of collection.

In the laboratory, macrobenthic animals were removed from the sample using forceps and preserved with 70% ethanol. The organisms were identified under a stereomicroscope and sorted to species or genera. The organisms of various taxonomic groups were weighed after gently blotting with filter paper to derive their wet weight (WW). Then, areal biomass concentration of each taxonomic group, g m^{-2}, was obtained by dividing its wet mass by the area of the sampler quadrate.

For fatty acid (FA) and organic carbon analyses, live individuals of particular taxa were withdrawn from the samples during the sorting, if the numbers were high enough to pool them and obtain an appropriate biomass (≥ 10 mg WW). Pooled samples for Chironomidae larvae and Oligochaeta could include several species. In the case of Ephemeroptera, Trichoptera, Hirudinea and Gastropoda most samples were comprised a single species or genus. Samples of Amphipoda were, as a rule, a mix of two species. The live animals were placed into beakers with filtered water of a temperature close to the field for 24 h to allow their gut contents to empty.

Then individuals of each sample were subdivided in two sub-samples for FA and carbon analyses. For FA analyses the animals were placed in chloroform-methanol mixture (2:1, v/v) and kept frozen (−20 °C) until analysis. Animals of the other sub-samples were wet weighed, dried until constant weight at 75 °C, and dry weighed to measure moisture content of a given taxa. The dried biomass was kept in a desiccator for further organic carbon analyzed.

Lipid extraction and preparation of fatty acid methyl esters (FAMEs) were the same as in our previous works (e.g., Kalachova et al., 2011). A gas chromatograph equipped with a mass spectrometer detector (6890/5975C,"Agilent Technologies", USA) and with a capillary HP-FFAP column was used. The instrument conditions were described in the above paper. Data were collected and analyzed using the GC ChemStation program ("Agilent Technologies", USA). The FAMEs were quantified according to peak area of the internal standard, nonadecanoic acid, which solutions were added to samples prior the lipid extraction. The samples for total organic carbon were analyzed with a Flash EA 1112 NC Soil/MAS 200 elemental analyzer (ThermoQuest, Italy).

Water samples for soluble nutrients were filtered through pre-cleaned membrane filters with pore diameter of 0.45 μm (Vladypor, Russia) and analyzed on the day of sampling. Inorganic phosphorus was determined by the ammonium-molybdate method on a spectrophotometer at 680 nm. Ammonia nitrogen was determined by the nesslerization method, at 425 nm. Nitrate nitrogen was measured by reduction into nitrite form onto a cadmium column followed by the reaction with sulfanilamide and naphthylamine and spectrophotometry at 530 nm.

To measure the between-river β-diversity in the macroinvertebrate assemblages the Sorensen similarity index was calculated like in similar studies (Woodward et al., 2010).

Daily production, P_D (g m^{-2} day^{-1}), was calculated by the formula:

$$P_D = G\,B$$

where G (day^{-1}) is the daily instantaneous growth rate and B (g m^{-2}) is biomass (WW). Values of G for arthropods were calculated according to the following formula:

$$G = a\,e^{bT}$$

where a and b are taxon-specific constants (Table 2) and T is temperature, °C. Daily instantaneous growth rates for Oligochaeta, Hirudinea and Gastropoda were calculated as follows:

$$G = G_{20} / 2^{0.1\,(20-T)}$$

where G_{20} is taxon-specific constant (Table 2).

Seasonal production for the each zoobenthos taxon, P_S, was calculated by trapezium method of integration:

$$P_S = \sum_{i=1}^{n} \frac{P_{Di} + P_{Di+1}}{2} \cdot (t_{i+1} - t_i)$$

where t is time (days). Since the integrated time spans in 2012 and 2013 were 128 and 125 days, respectively, P_S of 2013 was recalculated for 128 days by multiplying by 128/125 ratio. P_S values were converted to carbon units using average taxon-specific moisture and carbon contents. To calculate EPA and DHA seasonal production, the secondary production in carbon units (g C m^{-2} 128 days) for each taxon was multiplied by the average taxon-specific HUFA/C ratio (mg g^{-1}). Then, secondary production of biomass of all taxa, as well as EPA and DHA taxon-specific production were summarized to obtain the total production values. Weighted average temperature and biomass were also calculated for the studied periods of 2012 and 2013 by the trapezium method of integration.

Standard errors, one-way ANOVA and Tukey HSD *post-hoc* test (Brown, 2005) were calculated conventionally, using STATISTICA software, version 9.0 (StatSoft, Inc.).

RESULTS

Average water temperatures and concentrations of inorganic nutrients (ammonium and nitrate nitrogen, and inorganic phosphorus) are given in Table 1. The most profound difference in average seasonal temperatures, 6.1 °C, was between the Yenisei River (left bank) and the Mana River. The sampling site 2 of the Yenisei was affected by the Mana River discharge (Fig. 1) and thereby had a bit higher values of water temperature than the left-bank site (Table 1). In general, the Kacha River appeared to be richer in inorganic nutrients compared to the other studied rivers.

The species richness in the two warm rivers was evidently higher, than that in the Yenisei River (Table 3). Concerning abundant taxa, Amphipoda were found only in the Yenisei River, while Hirudinea occurred only in the warm rivers, Mana and Kacha, and Chironomidae were the most species-rich group (Table 3).

In the Yenisei River two amphipod species had the highest frequencies (Table 4), and they constituted most part of total biomass, up to 92.7%. In the Mana River Chironomidae larvae *Thienemannimya* sp. had the highest frequency, followed by Ephemeroptera larvae *Ephemera orientalis* (Table 4).The latter taxa dominated in biomass of zoobenthos: 56.6% and 38.4% in 2012 and 2013, correspondingly (Fig.2). In the Kacha River Chironomidae larvae *Orthocladius thienemanni* was the most frequently occurred species (Table 4), while Ephemeroptera larvae were dominant in the total biomass (Fig.2).

Species overlap between the river communities (β-diversity) according to Sorensen similarity index was the highest for the Yenisei sites (Table 4). The warm rivers, Mana and Kacha, also had comparatively high similarity index, while they were weakly similar to the Yenisei sites.

We used one-way ANOVA to estimate inter-site variation (effects) of EPA content in each taxa. We excluded from the analysis the taxa occurred only in one or two habitats or those that occurred sporadically. For Oligocheta, Ephemeroptera and Trichoptera, there was no statistically significant effect of river habitat on the EPA content (Fig.3). Chironomids inhabited sites of the Yenisei River, primarily *Prodiamesa olivacea* (Table 4), had significantly higher EPA contents (Fig.3) than those from the Mana River and the Kacha River, primarily *Microtendipes pedellus* and *Orthocladius thienemanni* (Table 4).

DHA contents per wet weight in most taxa, except Amphipoda, were negligibly small and thereby were not included in the ANOVA. Contents of DHA in Amphipoda from site 1 and site 2 did not differ significantly: $F = 2.46$, $P = 0.1374$.

Since there were no statistically significant differences in HUFA contents of the same taxa inhabited the studied rivers, we combined the biochemical data from all the sites and calculated the averages of HUFA contents for all the studied taxa (Table 5). The only exception was chironomids (Fig. 3), which were subdivided into two groups, Chironomidae 1-2 and Chironomidae 3-4, according to the sampling site numbers (Fig.1). There were overall statistically significant differences among taxa in HUFA per cents and contents according to one-way ANOVA (Table 5). Chironomidae 1-2 had the highest EPA level and content, followed by Limoniidae and Ephemeroptera, and Amphipoda had the highest DHA level and content (Table 5).

In the Yenisei River, left bank, there was the highest biomass and production in spite of the lowest water temperature (Table 6). In turn, production in the Kacha River was higher than that in the Yenisei River, right bank and in the Mana River in the both seasons, although values of biomass at these sites were comparable (Table 6). Production of EPA and especially DHA at the coldest site 1 also had the highest values in both seasons (Table 6). However, ratios of EPA

production to the biomass production, P_{EPA}/P_S, in all sites were comparable. In contrast, values of P_{DHA}/P_S in the Yenisei River, at both sites, were evidently higher than those in the warm rivers (Table 6).

Average values of EPA production for two seasons in the Yenisei River, site 1, were significantly higher, than those at the other sites after ANOVA (Fig. 4). The average EPA production in the Kacha River was significantly higher than that in the Yenisei River, site 2, and the Mana River. The highest average DHA production occurred in the coldest site 1, and its value at site 2 with the intermediate water temperature also was significantly higher, than those in two warm rivers (Fig. 4).

DISCUSSION

Our 'natural experiment' confirmed that although the Yenisei has a big reservoir upstream and is a substantially larger river than its tributaries, the Mana and Kacha, their hydrochemical characteristics, e.g. inorganic nutrient contents, are rather similar. Moreover, dominant primary producers in all the rivers, benthic (epilithic) microalgae, were represented by the same taxonomic groups, diatoms and greens.

In contrast to hydrochemical characteristics, the summer temperatures strongly contrasted in the Yenisei versus the Mana and the Kacha rivers, up to 12.2 ^{o}C. This contrast seems to be one of the main causes of some differences of species composition of the diatom and green microalgae, as well as in zoobenthos in the cold-water Yenisei and the warm-water Mana and Kacha (Table 1, 3-4).

We assessed if differences in species composition of biofilms in the studied rivers could affect food quality for benthic animals concerning levels of the omega-3 HUFA and their precursor, α-linolenic acid (ALA). All the dominant genera of greens, *Ulothix*, common for the Yenisei River, both banks, and the Mana River, and *Cladophora*, common for the Yenisei River, right bank, and the Kacha River, are known to have high levels of ALA (Torres-Ruiz et al., 2007; Sushchik et al., 2010). Diatom species of the Yenisei River, for instance, *Didymosphenia geminate,* are especially rich in EPA (Sushchik et al., 2010), and they also occurred in the Mana River and the Kacha River. Moreover, periphyton communities where warm-water *Melosira varians* dominated, like in the Mana and Kacha, also had high EPA levels (Huggins et al., 2004; Hill et al., 2011). Hence, diatom-green epilithic communities occurred in the cold-water Yenisei and in the warm-water Mana and Kacha rivers, appeared to be equally good sources of the omega-3 fatty acids for zoobenthos.

The increase in species richness of zoobenthos (α-diversity) in the two warm rivers relatively to the cold-water river, is in a good agreement with data of some other authors that global warming will lead to higher local and regional richness of freshwater benthic macroinvertebrate assemblages (Oertli et al., 2008; Floury et al., 2013). The studied warm and cold communities had slight similarity (β-diversity), although they were within a relatively small area and thereby had no biogeographical and dispersal constraints. In similar studies of Icelandic geothermal streams clear changes in both macroinvertebrate community structure and diversity with temperature were also found (Friberg et al., 2009).

Our first hypothesis, that in the cold river the same taxa have higher levels of EPA and DHA than those in warm rivers, was confirmed only for Chironomidae. The other studied taxa had similar HUFA contents, in spite of only partial overlapping of species in the habitats. Different species of Hirudinea occurred in the Kacha and Mana, but had nearly identical HUFA contents. The similarity of HUFA contents in spite of different habitats within the same taxa at the level of orders (Ephemeroptera, Trichoptera) and even subclasses (Oligochaeta, Hirudinea) appeared to be in good agreement with recent finding, that namely phylogenetic factor primarily controls fatty acid composition of aquatic invertebrates (Makhutova et al., 2011; Lau et al., 2012). However, we found the differences in EPA contents at the lower taxonomic level, namely within Chironomidae family. The dominant chironomid of the Yenisei, *Prodiamesa olivacea*, is evidently cold-water affiliate, like other Diamesinae (Woodward et al., 2010), and has the highest EPA content. Thus, the question concerning phylogenetic vs environmental regulation of fatty acid composition of aquatic invertebrates seems to be still on the table.

Our second hypothesis that in the cold river taxa with higher HUFA contents are more abundant was confirmed for DHA only. Indeed, in both sites of the Yenisei River Amphipoda with the highest DHA content were the dominant species. In the warm rivers, the taxa with the lowest DHA contents, Ephemeroptera and Limoniidae, were abundant.

In general, contents of HUFA in zoobenthos in the studied rivers were close to those reported in literature for the same freshwater taxa: insect larvae (Torres-Ruiz et al., 2007; Makhutova et al., 2011; Sánchez-Muros et al., 2014), Amphipoda (Kolanowski et al., 2007; Czesny et al., 2011), Oligochaeta (Goedkoop et al., 2000; Torres-Ruiz et al., 2007) and Hirudinea (Lau et al., 2012). However, Lau et al. (2012) reported twice lower EPA percentages for Ephemeroptera and Trichoptera, and Shipley et al. (2012) reported ~5-fold lower percentages and ~9-fold lower contents per weight of this HUFA for Ephemeroptera. Like in our study all the above authors found high DHA contents in Amphipoda and negligible amounts of this HUFA in other zoobenthos taxa.

Our third hypothesis that production of HUFA by zoobenthos is higher in the cold river appeared to be true for DHA, and partly for EPA. Indeed, EPA production in the warm Kacha River was significantly higher, than that in colder site at right bank of the Yenisei River. However, in the coldest site at the left bank of the Yenisei River the highest production of EPA occurred.

EPA and especially DHA are known to be of key physiological importance for fish growth and development (Sargent et al., 1999; Tocher, 2003). Indeed, DHA composes up to ~30% of fish brain lipids (Shields et al., 1999), but capacity of most fish to synthesize this HUFA from short-chain precursors is very limited (Tocher, 2003). Thus, shortage in food supply of DHA significantly affects fish growth and development (Vizcaino-Ochoa et al., 2010; Zakeri et al., 2011). According to our data, in the warm rivers, standing stock and production of zoobenthos, as the main food supply for fish, had significantly lower DHA content.

In turn, fish are the main source of EPA and DHA for humans (Gladyshev et al., 2013). To prevent cardiovascular diseases and neural disorders personal daily intakes of EPA+DHA ca. 0.5 – 1.0 g are necessary for most people (Kris-Etherton et al., 2009; Harris et al., 2009). However, world wild fish catch and aquaculture production are limited, and at present humankind faces with deficiency of EPA and DHA in diet (Gladyshev et al., 2009). If our results are interpreted in a climate warming context we can predict a decrease of production of these HUFA in river ecosystems and thereby a diminishing of their supply for humans through fish. Indeed, there are indirect evidences that the loss of cold freshwater habitats may cause a decrease of biochemically valuable fish production. In Europe climate warming stimulates a shift from salmonids to percids, and from percids to cyprinids (Jeppesen et al., 2010). As generalized recently, average EPA and DHA content in fish biomass decreased significantly from salmonids to percids, and from percids to cyprinids (Gladyshev et al., 2013). Thus, fish of high nutritive value for humans, salmonids, which preferred cold habitats are substituted by fish of lower nutritive value. This tendency is explicit in the studied ecosystems: in the cold sites of Yenisei River salmonid Siberian grayling *Thymallus arcticus* Pallas is the dominant species (Zuev et al., 2011), while in the both warm rivers, Mana and Kacha, cyprinids Siberian dace *Leuciscus leuciscus baicalensis* (Dybowski) and gudgeon *Gobio gobio cynocephalus* (Dybowski) are the most abundant (Zapekina-Dulkeit & Dulkeit, 1961; Chugunova & Pronin, 2011).

According to our present data, the differences of EPA and DHA contents and production in zoobenthos of the cold and warm rivers were caused by the differences of species composition. This finding is in a good agreement with our previous data that water temperature affected contents of these HUFA in lake zooplankton via changing of community taxonomic structure (Gladyshev et al., 2011). Thus, the cold-adapted species, primarily Amphipoda, gave

higher standing stock biomass and higher production, which was more valuable concerning HUFA contents for organisms of higher trophic levels. Both species of amphipods, *E. viridis* and *G. fasciatus*, are invaders from the Baikal Lake, which is known by low annual temperatures (Gladyshev & Moskvicheva, 2002).

Many studies reported changes of structural characteristics, species composition and biodiversity caused by climate change. However, reliance on structure alone makes it difficult to prescribe ecosystem management or restoration actions for a specific ecosystem service (Palmer & Febria, 2012). We tried to convert the changes of species composition of macrozoobenthos to the specific service of aquatic ecosystems: production of HUFA. We found that increase of biodiversity of river zoobenthos with the increase of water temperature, occurred like in other studies, was not accompanied by increase of HUFA production. On the contrary, the less diverse cold-water community gave the highest production of EPA and DHA. Thus, our 'natural experiment' gave an evidence of the strong effect of temperature on HUFA production by river zoobenthos, in the absence of the confounding effects (e.g. biogeography, seasonality and physico-chemical conditions). Basing on the data obtained we can predict that a climate warming can diminish DHA and partly EPA production by river zoobenthos with possible negative consequences for organisms of progressively higher trophic levels.

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552

553 **Table 1.** Physico-chemical parameters (means ± standard errors, n=10, May-September 2012-
554 2013) and abundance of epiphytic algal and cyanobacterial taxa in the studied sites. Biotic
555 parameters were estimated according to literature data: the Yenisei River, left bank (Sushchik et
556 al., 2010); the Yenisei River, right bank (Gaevsky et al., 2006); the Mana River (Anufrieva et al.,
557 2008); the Kacha River (Gold et al., 2005).

Characteristics	Yenisei, left bank	Yenisei, right bank	Mana	Kacha
Temperature (^{o}C)	8.4±0.8	11.7±0.8	14.5±1.6	14.2±1.7
Ammonium nitrogen (mg N L^{-1})	0.10±0.02	0.13±0.04	0.12±0.03	0.27±0.06
Nitrate nitrogen (mg N L^{-1})	0.14±0.04	0.05±0.01	0.10±0.03	0.25±0.05
Inorganic phosphorus (mg P L^{-1})	0.010±0.002	0.006±0.001	0.005±0.001	0.019±0.004
Bacillariophyta				
Cocconeis placentula Ehr.	++	++	++	
Diatoma tenuis (Lyngb) Ag.	++	++	++	+
Diatoma vulgare Bory				++
Didymosphenia geminata (Lyngb.) M.Schmidt	+++	+	++	+
Melosira varians C.Agardh			+	+
Navicula sp.	+	++	+	+
Rhoicosphenia abbreviate(Kütz.) Grun.	+++	+++	++	
*Synedra ulna (*Nitzsch) Ehr		+	++	+
genus *Cymbella*	++	++	+++	+++
genus *Fragilaria*	+	+	+	
genus *Gomphonema*	+++	+++	++	
Chlorophyta				
Cladophora glomerata (L) Kütz.		+	+	+++
Spyrogyra sp.			++	
Ulothrix zonata Kütz.	++	++	+	
Cyanophyta				
Oscillatoriaceae	+	+		+

558
559 +++ often occurred at high biomass
560 ++ often occurred at moderate biomass or sporadically occurred at high biomass
561 + often occurred at low biomass or sporadically occurred at moderate biomass

562 **Table 2.** Constants for calculation of daily instantaneous growth rate of freshwater zoobenthos.
563

Taxon	*a*	*b*	G_{20}	Reference
Oligochaeta			0.030	Berezina, 2008
Hirudinea			0.034	Nikolaev, 1980
Amphipoda	0.0160	0.009		Berezina, 2008
Odonata	0.0075	0.080		Golubkov, 2000
Ephemeroptera	0.0130	0.099		Golubkov, 2000
Trichoptera	0.0130	0.054		Golubkov, 2000
Plecoptera	0.0166	0.028		Golubkov, 2000
Diptera*	0.0075	0.143		Golubkov, 2000
Chironomidae	0.0087	0.142		Golubkov, 2000
Gastropoda			0.032	Arakelova, 1999

564
565 *other, than Chironomidae
566

567 **Table 3.** Number of macrozoobenthos species at the sampling sites in May-September, 2012 and
568 2013. Number of samples at each site, n = 20.

Taxa	Yenisei, left bank	Yenisei, right bank	Mana	Kacha
Plathelminthes				
Turbellaria	1	0	0	0
Nemathelmintes				
Nematoda	0	0	0	2
Annelida				
Oligochaeta	3	5	6	5
Hirudinea	0	0	3	2
Arthropoda				
Crustacea				
Amphipoda	2	2	0	0
Insecta				
Odonata	0	1	2	0
Ephemeroptera	5	7	22	10
Trichoptera	3	5	17	8
Plecoptera	0	2	10	0
Diptera				
Chironomidae	14	20	40	29
Ceratopogonidae	0	1	1	1
Limoniidae	0	1	2	3
Tabanidae	0	0	0	1
Empididae	0	0	1	1
Simuliidae	0	0	1	0
Blephariceridae	0	0	1	0
Tipulidae	0	0	1	0
Mollusca				
Bivalvia	0	1	1	0
Gastropoda	0	1	3	1
Total	***28***	***46***	***111***	***63***

569
570

571 **Table 4.** List of species with high frequencies (F, % of the all samples taken at a given site) and
572 Sorensen similarity indexes for zoobenthos β-diversity between the sites. The frequency of a
573 species was considered as high if F ≥ 50% at least at one site. Number of samples at each site, n
574 = 20, May-September, 2012 and 2013.

Species	Frequency, %			
	Yenisei, left bank	Yenisei, right bank	Mana	Kacha
Oligochaeta				
Limnodrilus hoffmeisteri Claparede			10	70
Slavina appendiculata d'Udekem	50	25		
Stylodrilus herringianus Claparede			90	
Tubifex tubifex O.F.Muller	15	40	5	65
Amphipoda				
Eulimnogammarus viridis Dybowski	100	65		
Gmelinoides fasciatus Stebbing	20	90		
Ephemeroptera				
Baetis gr. *fuscatus*			50	40
Caenis pseudorivulorum Keffermüller			10	55
Choroterpes altioculus Kluge			70	
Ecdyonurus jornensis Bengtsson				65
Epeorus pellucidus Brodsky	5	25	70	15
Ephemera orientalis McL.	5	55	95	55
Ephemerella ignita Poda			50	40
Ephemerella lenokii Tshernova			70	10
Potamanthus luteus L.	5	60	80	
Rhithrogena lepnevae Brodsky			65	
Trichoptera				
Ceraclea exisa Morton			55	35
Lepidostoma hitrum Fabricius			75	
Psychomyia pusilla Fabr.			15	75
Sericostoma personatum Kirby et Spense			55	
Setodes sp.			80	
Chironomidae				
Cryptochironomus defectus Kieffer			15	55
Microtendipes pedellus De Geer	10	35	80	75
Orthocladius saxicola Kieffer			30	60
Orthocladius thienemanni Kieffer			85	100
Polypedilum bicrenatum Kieffer	5	15	10	50
Polypedilum scalaenum Schrank			80	55
Prodiamesa olivacea Meigen	75	25		5
Rheotanytarsus sp.			10	80
Stictochironomus crassiforceps Kieffer		10	5	85
Thienemannimya sp.			100	35
	Sorensen similarity indexes			
Yenisei,right bank	0.62			
Mana	0.12	0.19		
Kacha	0.16	0.24	0.46	

575

Table 5 Average (± standard errors) moisture and organic carbon contents and percentages (of total fatty acids) of eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) and their contents in biomass of zoobenthos taxa in the studied rivers in May-September, 2012 and 2013: *n* – number of samples for moisture and organic carbon analyses or fatty acid analyses (in parentheses) , *F* – Fisher's test for categorical predictor in one-way ANOVA and *P* – statistical significance of ANOVA results. Means labeled with the same letter are not significantly different at $P < 0.05$ after Tukey HSD *post-hoc* test.

Taxa	*N*	Moisture, % ww	C, % dw	EPA, %	DHA, %	EPA, mg g^{-1} ww	DHA, mg g^{-1} ww
Oligochaeta	7(15)	76.2 ± 1.6	41.5 ± 1.2	13.6 ± 1.0^{AB}	1.1 ± 0.2^{A}	1.48 ± 0.14^{A}	0.12 ± 0.02^{A}
Hirudinea	7(8)	80.5 ± 1.3	47.9 ± 0.6	15.7 ± 1.9^{AB}	0.6 ± 0.2^{ABD}	1.43 ± 0.30^{A}	0.06 ± 0.02^{A}
Amphipoda	19(17)	73.9 ± 1.2	38.0 ± 0.9	17.1 ± 0.7^{A}	3.2 ± 0.3^{C}	2.79 ± 0.37^{AB}	0.47 ± 0.05^{B}
Ephemeroptera	36(48)	78.0 ± 0.7	47.3 ± 0.8	16.8 ± 0.7^{A}	0.1 ± 0.0^{D}	3.64 ± 0.26^{BC}	0.02 ± 0.00^{C}
Trichoptera	14(23)	76.9 ± 1.9	47.8 ± 1.6	10.1 ± 1.3^{B}	0.3 ± 0.1^{BD}	3.03 ± 0.49^{A}	0.07 ± 0.01^{AC}
Plecoptera	6(8)	71.4 ± 2.9	48.4 ± 0.6	15.0 ± 1.9^{AB}	0.2 ± 0.1^{BD}	2.40 ± 0.39^{A}	0.05 ± 0.02^{AC}
Chironomidae 1-2	7(8)	76.9 ± 2.6	48.7 ± 1.4	19.4 ± 1.1^{A}	0.4 ± 0.1^{ABD}	5.21 ± 0.45^{C}	0.10 ± 0.02^{AC}
Chironomidae 3-4	10(13)	79.2 ± 1.9	45.5 ± 1.5	13.4 ± 1.9^{AB}	0.3 ± 0.1^{BD}	2.33 ± 0.36^{A}	0.05 ± 0.01^{AC}
Limoniidae	3(3)	83.4 ± 2.4	50.3 ± 0.2	19.6 ± 3.6^{AB}	0.2 ± 0.1^{ABD}	3.30 ± 1.85^{AC}	0.04 ± 0.02^{AC}
Gastropoda	4(5)	79.7 ± 2.6	37.5 ± 3.0	11.9 ± 1.2^{AB}	0.9 ± 0.3^{AB}	0.62 ± 0.11^{A}	0.05 ± 0.02^{AC}
F		-	-	4.79	67.34	6.03	46.80
P		-	-	0.00001	0.00000	0.00000	0.00000

Table 6. Weighted mean seasonal temperature (T, ^{o}C), weighted mean seasonal biomass of zoobenthos (B, g C m^{-2}), seasonal production of zoobenthos (P_S, g C m^{-2} 128 days), seasonal production of eicosapentaenoic acid (P_{EPA}, mg m^{-2} 128 days) and docosahexaenoic acid (P_{DHA}, mg m^{-2} 128 days) by zoobenthos and their ratios (mg g^{-1} C) in the studied rivers: S1 – the Yenisei River, left bank; S2 – the Yenisei River, right bank; S3 – the Mana River; S4 – the Kacha River.

Site, year	T	B	P_S	P_{EPA}	P_{DHA}	P_{EPA}/P_S	P_{DHA}/P_S
S1 2012	9.0	3.12	7.67	244.6	30.7	31.9	4.0
S1 2013	8.0	4.08	9.08	270.6	40.7	29.8	4.5
S2 2012	12.7	0.98	2.39	66.8	9.7	27.9	4.1
S2 2013	12.0	1.12	3.62	117.7	8.8	32.5	2.4
S3 2012	17.1	0.26	2.12	65.0	0.7	30.6	0.3
S3 2013	14.4	0.51	2.28	60.5	0.8	26.6	0.4
S4 2012	15.8	0.64	3.97	106.2	1.7	26.8	0.4
S4 2013	15.3	0.43	4.49	152.1	1.2	33.9	0.3

Figure legends

Fig. 1. Map of the studied area. Dam – the dam of Krasnoyarsk Hydroelectric Power Station. Dashed area indicates Krasnoyarsk city. Sampling sites: 1 – the Yenisei River, left bank; 2- the Yenisei River, right bank; 3 – the Mana River; 4 – the Kacha River.

Fig. 2. Average seasonal percent biomass (g m^{-2} ww) of quantitatively prominent zoobenthos taxa. Sampling site abbreviations: S1 – the Yenisei River, left bank; S2 – the Yenisei River, right bank; S3 – the Mana River; S4 – the Kacha River.

Fig. 3. Average content of eicosapentaenoic acid (EPA) in zoobentos taxa occurred in all the studied rivers, May-September, 2012 and 2013. Bars represent standard errors. Means labeled with the same letter are not significantly different from each other at $P<0.05$ after Tukey HSD *post hoc* test; absence of the letter labels indicates that ANOVA is not significant.

Fig. 4. Average seasonal production (May-September, 2012 and 2013, 128 days) of eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) by zoobenthos in the studied rivers: S1 – the Yenisei River, left bank; S2 – the Yenisei River, right bank; S3 – the Mana River; S4 – the Kacha River. Production values were calculated for single and triple zoobenthos biomass data in 2012 and 2013, respectively; then they were averaged, bars represent standard errors. Means labeled with the same letter are not significantly different from each other at $P<0.05$ after Tukey HSD *post hoc* test.